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Research Article

The impact of precipitation and temperature on seed ripening and germination dynamics of some meadow species of Western and Central Europe

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Abstract

Weather fluctuations can influence germination dynamics and pose a threat to the conservation of perennial lowland hay meadow species (Natura 2000 habitat code 6510). This study aims to assess the effects of temperature and precipitation changes on the germination performance of 23 plant species, divided into two harvest periods (July and late September/early October) of a two-year collection (2022–2023). The study classifies these species based on shared germination characteristics and identifies key parameters influencing germination performance. Germination tests were conducted in Petri dishes at 20 °C for 16 hours (dark) and 30 °C for 8 hours (light), with a light intensity of 1000 lux. Quantitative (GC - germination capacity, FUS - fresh ungerminated seeds, and DS - dead seeds) and qualitative (t_{50} – the half of germination time, T. Index - Timson index) aspects were analysed using a two-way ANOVA test. Results revealed significant interactions between species and weather conditions across both collection periods. Wetter conditions increased GC and shortened t_{50} associated with rising germination velocity in most species, while warmer and drier conditions prolonged t_{50} and increased DS share. Heatmap clustering revealed that several species, including *Tragopogon pratensis*, *Dianthus deltoides*, and *Centaurea jacea*, demonstrated stable germination performance, making these species promising candidates for restoration. The decision tree identified Timson index as the most influential parameter explaining GC. These findings demonstrate that understanding germination dynamics caused by climate change may aid conservation-oriented restoration efforts for native species, enabling the implementation of seed mixtures of introduced species and informed decisions on the optimal time for seed recruitment.

Key words: *Arrhenatherion* meadows, Germination capacity, Germination dynamics, Half of germination time, Maternal effects, Seed mixtures, Timson index

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Introduction

Natural and semi-natural grasslands are one of the major habitats that support numerous ecosystem services (Pisani et al. 2021; Schils et al. 2022), including water supply and nutrient regulation (Kayser and Isselstein 2004), carbon storage, erosion prevention, climate change mitigation, and pollination (Bengtsson et al. 2019). Grassland multifunctionality is driven by the diversity of plant communities,

including those in lowland hay meadows where *Arrhenatherion* meadows are therein (Habitat code: 6510 according to Annex I of the Habitats Directive (92/43/EEC) (European Commission 2021). In the phytosociological hierarchy, more than 36 plant communities of this meadow belong to the class of *Molinio-Arrhenetheretea* with *Arrhenatherion elatioris* as a plant alliance characterized by mesic, nutrient-moderate, and extensive mown and grazed lowland meadows (Rodríguez-Rojo et al. 2017). However, grassland intensification management, including early, low, and frequent mowing, fertilization, the use of selective herbicides to eliminate dicotyledonous plants, as well as high grazing pressure and conversion to arable land, has led to a reduction in seed production of native species in *Arrhenatherion* meadows (Scotton et al. 2009). Then, decreasing seed production has potentially affected plant succession timing specifically in lowland hay meadows (Janicka et al. 2021).

Those interrelated phenomena have also affected plant communities in lowland hay meadows (habitat code: 6510) in Poland, as reported by GIOŚ (2018), which compared four aspects (total area, functionality, conservation prospects, and conservation status) between 2009–2011 and 2016–2018. Land use change, intensive mowing, and grazing were the three primary factors responsible for the decrease. Those factors, combined with weather fluctuations (shifted from a wet period in 2016 to a dry period in 2018), led to inadequate (U1) functionality of *Arrhenatherion elatioris* meadows, and even to an unfavourable (U2) conservation status for many areas of this meadow under Natura 2000. The number of sites with a U1 rating decreased significantly, and the number of sites with a U2 rating almost doubled (GIOŚ 2018). Practically, extreme weather events (droughts and floods) may strongly drive farmers' decision-making regarding grassland management (Shipley et al. 2024).

The climatic projection for Europe predicts a temperature increase of 1.5 to 4 °C by 2080, accompanied by shifts in rainfall patterns (IPCC 2014). Consequently, plants should rapidly adapt to maintain habitat resilience in the face of unpredictable adverse weather conditions (Veselá et al. 2020). Changes in temperature and rainfall intensity can significantly affect soil moisture and relative humidity over large areas, directly affecting the establishment requirements of plant populations, such as germination and seedling growth (Carta et al. 2022). One potential negative effect could be a change in the proportion and timing of seed germination inherited by progeny from their mother plants, known as the maternal effect (Dudney et al. 2017).

Shifts in germination behaviour can gradually alter the fitness of plant communities and the capacity of the regeneration niche over time (Braz et al. 2016). For native plants, changes in the germination niche shape germination dynamics (Pedrini and Dixon 2020). Another study on some species of *Arrhenatherion elatioris* Koch 1926 meadow showed that the use of germination dynamics as a tool for selecting target species for restoration has not been fully explored, due to the sensitivity of germinability to weather changes (Janicka et al. 2021). Therefore, the implementation of conservation-oriented restoration should be considered to save the high natural value of native species (Volis 2019) and their vegetation, especially for endemics (Bruchmann and Hobohm 2010; Rodríguez-Rojo et al. 2017; Perrino et al. 2024) or those of conservation interests (Garcia 1992; Perrino et al. 2023; Cordier et al. 2025).

Nowadays, global restoration is facing limitations in preserving the gene pool of native species, making it crucial for the need for restoration linked to nature

conservation (Toma et al. 2023). Yet the importance of local species for conservation purposes in restoring degraded habitats is often overlooked due to species-specific reasons and environmental influences that affect seed germinability during seed maturation (Barr et al. 2017). Seed maturation plays a role in controlling the germination of progeny, as mature seeds can inherit germination-linked genes from mother plants that were activated under specific germination requirements (Chahtane et al. 2017). Thus, assessing the germination performance of local species should incorporate multiple aspects, including the number of germinated seeds and quality aspects (germination time and speed), which reveal the maternal effect in progenies and help overcome this effect in the field (Pedrini and Dixon 2020).

The study fills an important knowledge gap regarding the germination dynamics of *Arrhenatherion* meadow species, driven by maternal effects, and changes in germination efficiency under variable climatic conditions, with implications for conservation and restoration. Therefore, this study has three objectives: (1) to assess the effect of weather variability between species from two harvest years on germination performances, (2) to identify species based on common germination characteristics, and (3) to identify key parameters influencing germination performances through decision tree analysis. This study also hypothesizes that: (1) seasonal weather variations in different harvest years influence the germination dynamics of species, (2) species with similar germination performance tend to belong to the same specific group, and (3) germination performance does not depend equally on all aspects of germination but may rather be determined by a specific aspect of the germination quality and quantity.

Materials and methods

Temperature and precipitation monitoring

The meteorological data included temperature and precipitation over five months in 2022 and five months in 2023, i.e., from June to October in both years (Fig. 1). The period for weather recording was determined by the seed maturation period of the studied species, which was at least a month prior to the collection time.

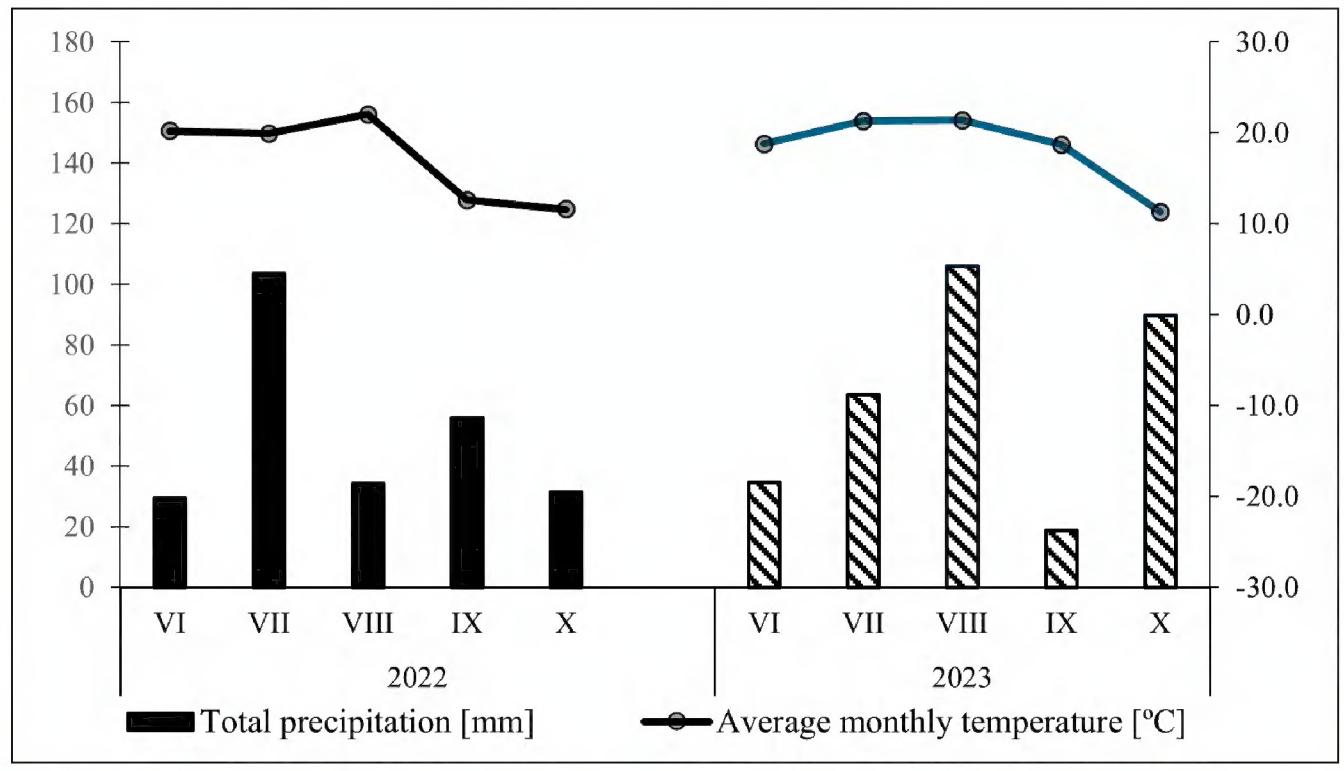


Figure 1. Meteorological data: Bar plots refer to total precipitation (mm) and line plots refer to average monthly temperature (°C) from June to October for the years 2022 and 2023

Study sites and seed collection

Mature seeds of 23 studied species were collected from three different meadows in the Mazovian Voivodeship (Table 1). Seeds of non-forest habitat species, characteristic of the Molinio-Arrhenatheretea class (19 of 23

Table 1. Phytosociological units, time, and place of collection of the 23 studied meadow species.

Phytosociological units/Species	Species abbreviation	Botanical family	Collection time	Location and geographical coordinates
Molinio-Arrhenatheretea (Class)				
Alopecurus pratensis L.	Ap	Poaceae	July	Mniszew (Long 51.85 Lat 21.267)
Centaurea jacea L.	Cj	Asteraceae	September/ October	Tymoteuszew (Long 52.25 Lat 21.65)
Lathyrus pratensis L.	Lp	Fabaceae	July	Solec (Long 52.05 Lat 21.083)
Plantago lanceolata L.	Pl	Plantaginaceae	July	Mniszew (Long 51.85 Lat 21.267)
Molinietalia (Order)				
Sanguisorba officinalis L.	So	Rosaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Silene flos-cuculi (L.) Greuter & Burdet	Sf	Caryophyllaceae	July	Mniszew (Long 51.85 Lat 21.267)
Molinion caeruleae (Alliance)				
Briza media L.	Bm	Poaceae	July	Tymoteuszew (Long 52.25 Lat 21.65)
Galium boreale L.	Gb	Rubiaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Succisa pratensis Moench	Sp	Caprifoliaceae	September/ October	Tymoteuszew (Long 52.25 Lat 21.65)
Cnidion dubii (Alliance)				
Allium angulosum L.	Aa	Amaryllidaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Kadenia dubia (Schkuhr) Lavrova & V.N.Tikhom.	Kd	Apiaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Arrhenatheretalia (Order)				
Achillea millefolium L.	Am	Asteraceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Leucanthemum vulgare Lam.	Lv	Asteraceae	July	Mniszew (Long 51.85 Lat 21.267)
Arrhenatherion (Alliance)				
Campanula patula L.	Cp	Campanulaceae	July	Tymoteuszew (Long 52.25 Lat 21.65)
Geranium pratense L.	Gp	Geraniaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Knautia arvensis (L.) Coult.	Ka	Caprifoliaceae	July	Tymoteuszew (Long 52.25 Lat 21.65)
Tragopogon pratensis L.	Tp	Asteraceae	July	Solec (Long 52.05 Lat 21.083)
Arrhenatheretum elatioris (Ass.)				
Arrhenatherum elatius (L.) P.Beauv. ex J.Presl & C.Presl	Ae	Poaceae	July	Mniszew (Long 51.85 Lat 21.267)
Lolio-Cynosuretum (Ass.)				
Scorzoneroides autumnalis (L.) Moench	Sa	Asteraceae	July	Solec (Long 52.05 Lat 21.083)
Others				
Dianthus deltoides L.	Dd	Caryophyllaceae	July	Mniszew (Long 51.85 Lat 21.267)
Eryngium planum L.	Ep	Apiaceae	July	Mniszew (Long 51.85 Lat 21.267)
Hypericum perforatum L.	Hp	Hypericaceae	September/ October	Mniszew (Long 51.85 Lat 21.267)
Vicia angustifolia L.	Va	Fabaceae	July	Mniszew (Long 51.85 Lat 21.267)

Note: Species names were given according to the Royal Botanic Gardens Kew (2025) (Plants of the World Online | Kew Science, accessed on 28.07.2025). Phytosociological units were given according to Matuszkiewicz (2012).

species), and abundant in these areas, were collected. The remaining four species, although representing other phytosociological units, were also collected because they occurred in abundance in the study areas. Seed collections were carried out in July 2022 and 2023 (14 species) and in early October 2022 or late September 2023 (9 species).

Germination test

After the seed collection activity, the collected seeds were cleaned of inert matter and other debris particles, stored in paper bags, and kept at approximately 20 °C (room temperature) until the germination test was conducted. Based on the International Seed Testing Rules (ISTA 2018), the germination test was performed under a specific photoperiod regime (20 °C for 16 hours (darkness) and 30 °C for 8 hours (light); 1000 lux under an LED lamp). One hundred and fifty seeds were used for each species, which were divided into three replicates of 50 seeds each (3 repetitions by 50 seeds). Seeds were set up in 94 mm plastic Petri dishes containing moistened Whatman No. 1 filter paper soaked in 1.5 mL of distilled water. After that, plastic Petri dishes containing seeds were secured with parafilm and placed in the versatile environmental test chamber (PHcbi Model no.MLR-352H-PE; Made in Japan). The test was conducted from the end of January to March 2023 (collection in 2022) and from the end of November to January 2024 (collection in 2023). Germination counts were recorded every other day for 34 days, during which germinated seeds were extracted after counting. Germinated seeds were identified by a visible radicle protrusion (1 mm) observed by the eye or under a magnifying glass (ISTA 2018).

Formula for germination characteristics

GC

ISTA (2018) defines the percentage of seeds in a batch or replicate capable of germinating under optimal conditions as germination capacity (GC), as follows:

$$\mathrm{GC} = \frac{Number\ of\ seeds\ germinated}{Total\ number\ of\ seeds\ tested} \times 100\% \quad (1)$$

FUS and DS

According to ISTA (2018), the FUS embryo remains viable and green, without any decay or infection by fungi or other seed-borne pathogens. On the other hand, DS is characterized by a soft seed coat, as the decomposition of the embryo inside the seed by fungi or other seed-borne pathogens renders the embryo inviable. The formula for both traits is similar to the formula for germination capacity, with a change in the number of FUS or DS.

The half-time of germination (t_{50})

Total germination days means the time span or duration from initial germination to its completion. The initial germination time refers to the point in time

when the seed first sprouts. According to Farooq et al. (2004), the time required to obtain 50% of the number of seeds germinated is called the half-time of germination or t_{50}, and has the formula:

$$t_{50} = T_i + \frac{\left(\frac{N+1}{2} - n_i\right)(t_j - t_i)}{n_j - n_i} \quad (2)$$

Where: N - the final number of germinating seeds, and n_i and n_j - the cumulative number of seeds germinated by adjacent counts at specified t_i and t_j, respectively, when $N_i < \frac{N}{2} < N_j$.

Timson index ($T.\ Index$)

We used the modified Timson Index formula proposed by Khan and Ungar (1984) to calculate the germination velocity (rate). This index quantifies the germination rate, with higher values indicating faster germination, and its value is defined as a percentage (%):

$$T.Index = \sum \frac{G}{T} \quad (3)$$

Where: G - percentage of seeds germinated in a specific time interval, and T - total number of germination days.

Data analysis

R Studio 4.4.1 and Microsoft Excel were used to analyse germination data. All studied species were divided into two groups based on the month of collection, allowing for further analysis. All germination parameters were calculated by loading the "germinationmetrics" package in R Studio. First, a two-way analysis of variance (ANOVA) was used to evaluate germination dynamics in terms of quantity (GC, FUS, and DS) and quantitative aspects (t_{50} and T. Index). Parameters expressed as percentages (GC, FUS, DS, and T. Index) were transformed to the arcsine form to meet the requirements of normality and homoscedasticity. Species was the first factor, and weather data was the second. In case of significant interaction effects, LSD (Least Significant Difference) post hoc tests were used. The "agricolae", "emmeans", "multcomp", and "multcompView" packages were used for the analysis. Clustering plots in the form of heatmaps with standardized Z-scores were created to examine species migration within groups based on changes in germination efficiency. This analysis was visualized using the "pheatmap" package. To select the most important germination trait and the corresponding species, two decision trees from the 2023-year collection (July and September) were developed and visualized using the "rpart" and "rpart.plot" packages, aiming to propose species for composing seed mixtures for the field experiment.

3. Results

a. Interaction of species with weather conditions during seed ripening

The seed germination properties of the tested species were analysed using two-way analysis of variance (ANOVA). The interplay of species with various

weather conditions is presented in Table 2 (for July collection) and Table 3 (for September/October collection).

The obtained post hoc LSD results (Fig. 2A) for 14 species collected in July indicate that the 3 Poaceae species (*A. elatius*, *A. pratensis*, and *B. media*) showed the

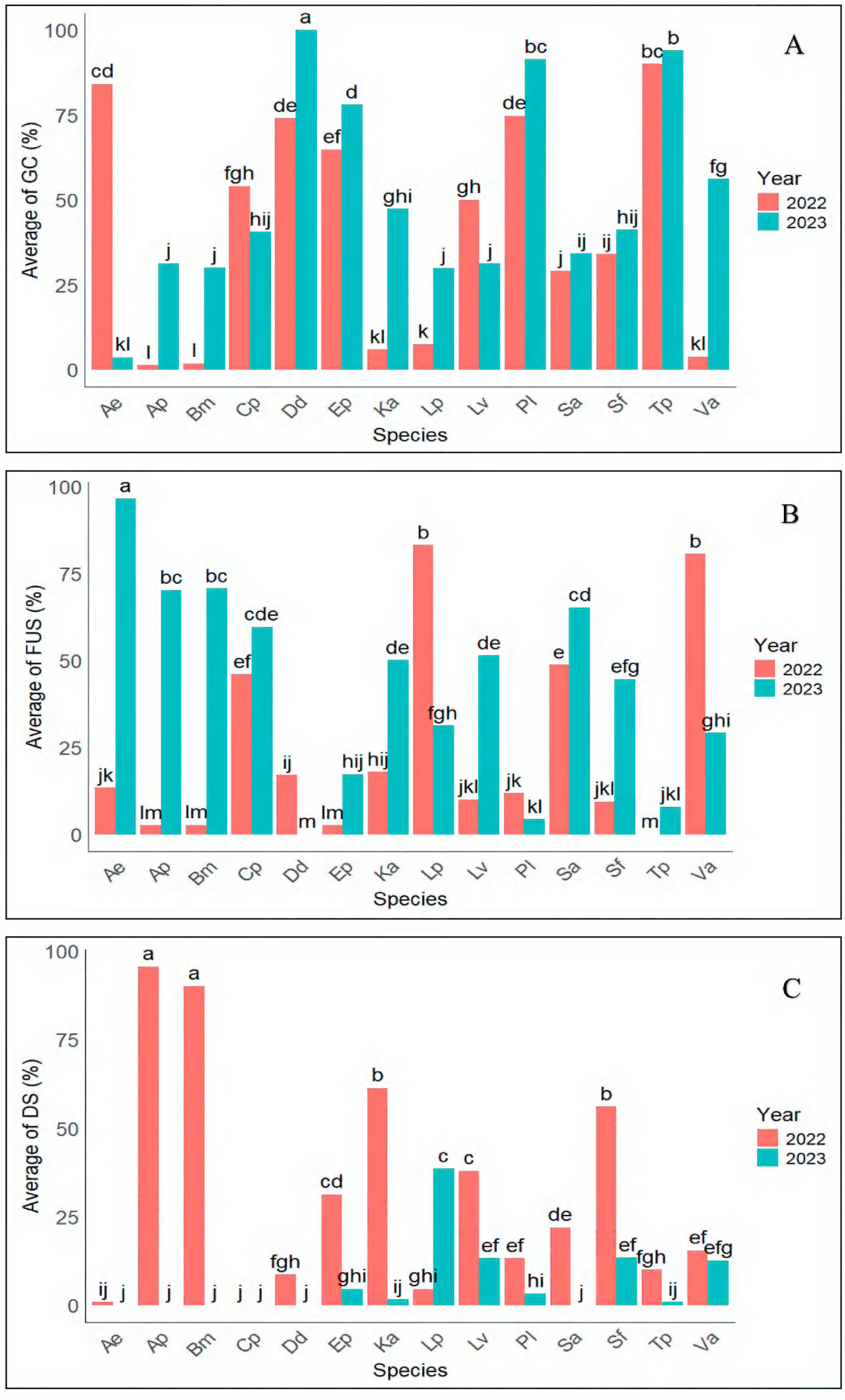

A
Average of GC (%)
100
75
50
25
0
cd kl l j l j fgh hij de a ef d kl ghi k j gh j de bc j ij ij hij bc b kl fg
Year
2022
2023
Ae Ap Bm Cp Dd Ep Ka Lp Lv Pl Sa Sf Tp Va
Species
B
Average of FUS (%)
jk lm lm ef cde ij m lm hij hij de b fgh jkl jk kl e cd jkl efg m jkl b ghi
C
Average of DS (%)
ij j a j a j j j fgh j cd ghi b ij ghi c c ef ef hi de j b ef fgh ij ef efg

Figure 2. Quantitative germination characteristics of the species collected in July. **A.** Germination Capacity (GC in %); **B.** Fresh Ungerminated Seeds (FUS in %), and **C.** Dead Seeds (DS in %). The same letter indicates non-significant differences according to the LSD post hoc test at $p < 0.05$. The full names of the species are given in Table 1.

Table 2. Two-way analysis of variance (ANOVA) of seed germination parameters for 14 species collected in July 2022 and 2023.

Parameter	Species		Weather		Species: Weather	
	Df	*p*-value	Df	*p*-value	Df	*p*-value
GC	13	< 2E-16***	1	7.98E – 12***	13	< 2E-16***
FUS	13	< 2E-16***	1	4.85E – 14***	13	< 2E-16***
DS	13	< 2E-16***	1	< 2E-16***	13	< 2E-16***
t_{50}	13	4.01E – 07***	1	0.0022**	13	0.02*
T. Index	13	< 2E-16***	1	6.48e – 11***	13	< 2E-16***

Explanations: GC – Germination Capacity, FUS – Fresh Ungerminated Seed, DS – Dead Seed, t_{50} – the median germination time, T. Index – Timson Index. Df – Degree of freedom, *p*-value is significant at *p<0.05; **p<0.01; ***p<0.001.

Table 3. Two-way analysis of variance (ANOVA) of seed germination parameters for 9 species collected in September/October 2022 and 2023.

Parameter	Species		Weather		Species: Weather	
	Df	*p*-value	Df	*p*-value	Df	*p*-value
GC	8	< 2E-16***	1	0.609^{ns}	8	1.21E - 07***
FUS	8	1.06E - 11***	1	0.292^{ns}	8	0.0003***
DS	8	1.25E - 12***	1	0.613^{ns}	8	2.71E - 05***
t_{50}	8	0.00013***	1	0.967^{ns}	8	0.002**
T. Index	8	< 2E-16***	1	0.739^{ns}	8	1.25E - 10***

Explanations: GC – Germination Capacity, FUS – Fresh Ungerminated Seed, DS – Dead Seed, t_{50} – the median germination time, T. Index – Timson Index. Df – Degree of freedom, ns – non-significant at p<0.05; *p*-value is significant at *p<0.05; **p<0.01; ***p<0.001.

opposite trend, with *A. elatius* having a remarkable decrease in GC share (from approximately 86% in 2022 to 4% in 2023). Three species: *T. pratensis*, *S. autumnalis*, and *S. flos-cuculi* showed a slight increase, while the remaining species collected in 2023 exhibited a significant increase in GC, except for *A. elatius*, *C. patula*, and *L. vulgare*. Interestingly, three grass species also showed the highest proportion of FUS (±90% for *A. elatius*, and ± 75.4% for *A. pratensis*, and *B. media*) in the 2023 collection (Fig. 2B). However, seeds of two legumes (*L. pratensis* and *V. angustifolia*) harvested in 2023 showed a significant decrease in the FUS share (±73% for both) compared to the 2022 harvest (approx. 27 and 24%, respectively). Most species collected in July decreased their DS share in the 2023 collection (Fig. 2C), except for *L. pratensis*, for which the DS share increased (from less than 25% to more than 40%), indicating that this phenomenon was influenced by weather factors.

Among seeds collected in September/October, the greatest significant increase in GC was observed in *G. pratense* and *H. perforatum*, collected in 2023 (13.3% and 38%, respectively), compared to 2022 (28% and 72.7%, respectively). *C. jacea* seeds represented the highest GC, which was at a similar level in both harvest years (Fig. 3A). In contrast to other species, seeds of *A. angulosum* (59.3%), *G. boreale* (12%), and *K. dubia* (16%) had a noticeable decrease in GC in the 2023 harvest year. Regarding the share of FUS (Fig. 3B), a reciprocal trend was observed between *H. perforatum* and *K. dubia* in both years of study, with a significant decrease in the share of FUS in *H. perforatum* seeds (42.6% in 2022 and 6% in 2023). In the case of *K. dubia*, the opposite trend was observed, with a significantly higher share of FUS in seeds from the 2023 collection (55.3%)

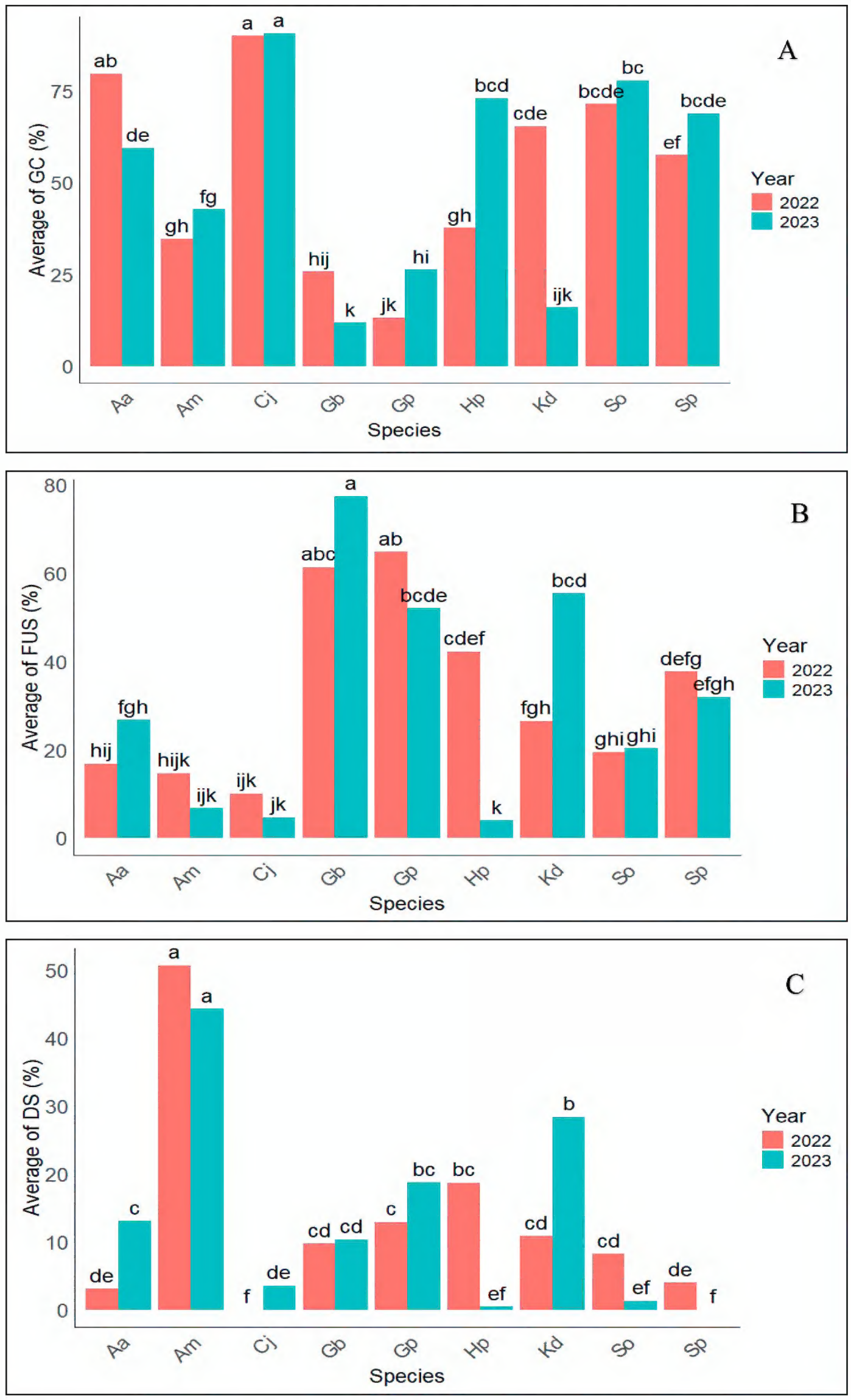


Figure 3. Quantitative germination characteristics of the species collected in September/October. **A.** Germination Capacity (GC in %); **B.** Fresh Ungerminated Seed (FUS in %), and **C.** Dead Seed (DS in %). The same letter indicates non-significant differences according to the LSD test at $p<0.05$. The full names of the species are given in Table 1.

compared to seeds from the 2022 collection (26.7%). The most significant increase in the share of DS (Fig. 3C) occurred in the case of seeds of three species (*A. angulosum*, *C. jacea*, and *K. dubia*) obtained in 2023, by approximately 13.3%, 5.3%, and 28.7%, respectively. Conversely, the proportion of DS in the

remaining three species (*H. perforatum*, *S. officinalis*, and *S. pratensis*) was significantly lower in 2023, amounting to 1.3%, 2%, and 0%, respectively.

Regarding the aspects of seed germination quality, including t_{50} and Timson Index, these varied by species and harvest year in both months. For instance, the t_{50} of seeds collected in July 2022 was longer than in 2023 (Fig. 4A) except for two grasses (*A. elatius* and *A. pratensis*) and one legume (*V. angustifolia*). Only two species had a dramatically reduced t_{50} in 2023 compared to 2022: *B. media* (from 16 to 5.9 days on average) and *K. arvensis* (from 16 to 6.7 days on average). In general, a longer t_{50} implies slower germination and vice versa, as represented by *A. elatius* with a significant decrease in the Timson index (from 36.9% per day in 2022 to 1.4% per day in 2023), followed by a moderate decrease in *L. vulgare* (from 21.6 to 14.7% per day) and last in *C. patula* (from 14.1 to 11.9% per day). The weather shift in 2023, primarily in June before the harvest in July, affects the faster T. Index compared to other harvests (Fig. 4B).

Seeds of *G. boreale* recorded the greatest reduction of t_{50} in 2023 (from 16.3 to 10.2 days) (Fig. 5A), in contrast to seeds of *G. pratense*, which recorded the greatest extension of t_{50} in the same year (from 6.8 to 19.5 days). Nevertheless, the seeds of these species were neither the fastest nor slowest in the Timson Index, as were the seeds of species collected in July (Fig. 5B). Instead, higher rainfall with lower

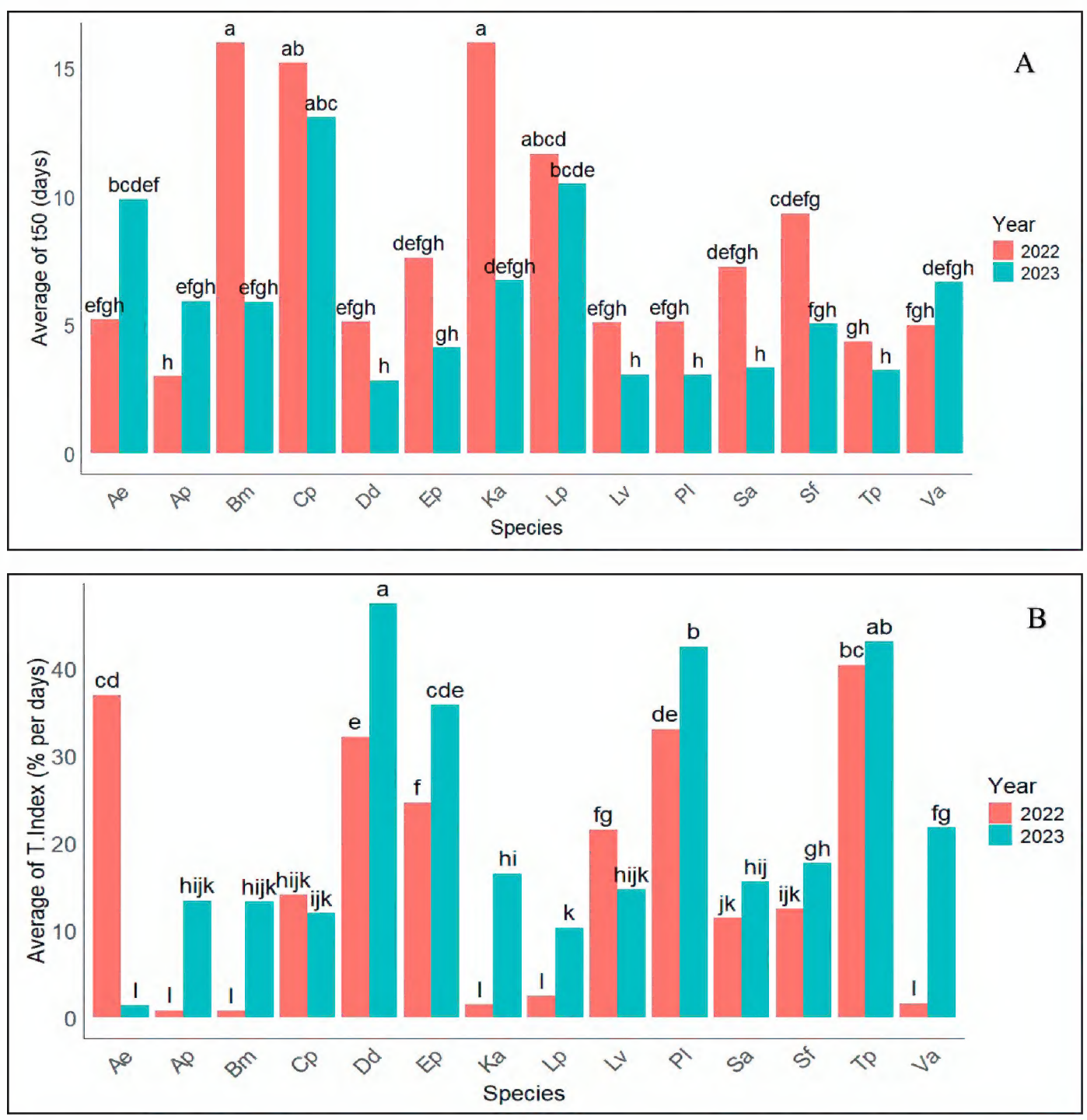


Figure 4. LSD bar plots of seed germination quality aspects of species collected in July 2022 and 2023. **A.** t_{50} or median germination time (days), and **B.** Timson Index (% per day). The same letter indicates non-significant differences according to LSD test at $p<0.05$. The full names of the species are given in Table 1.

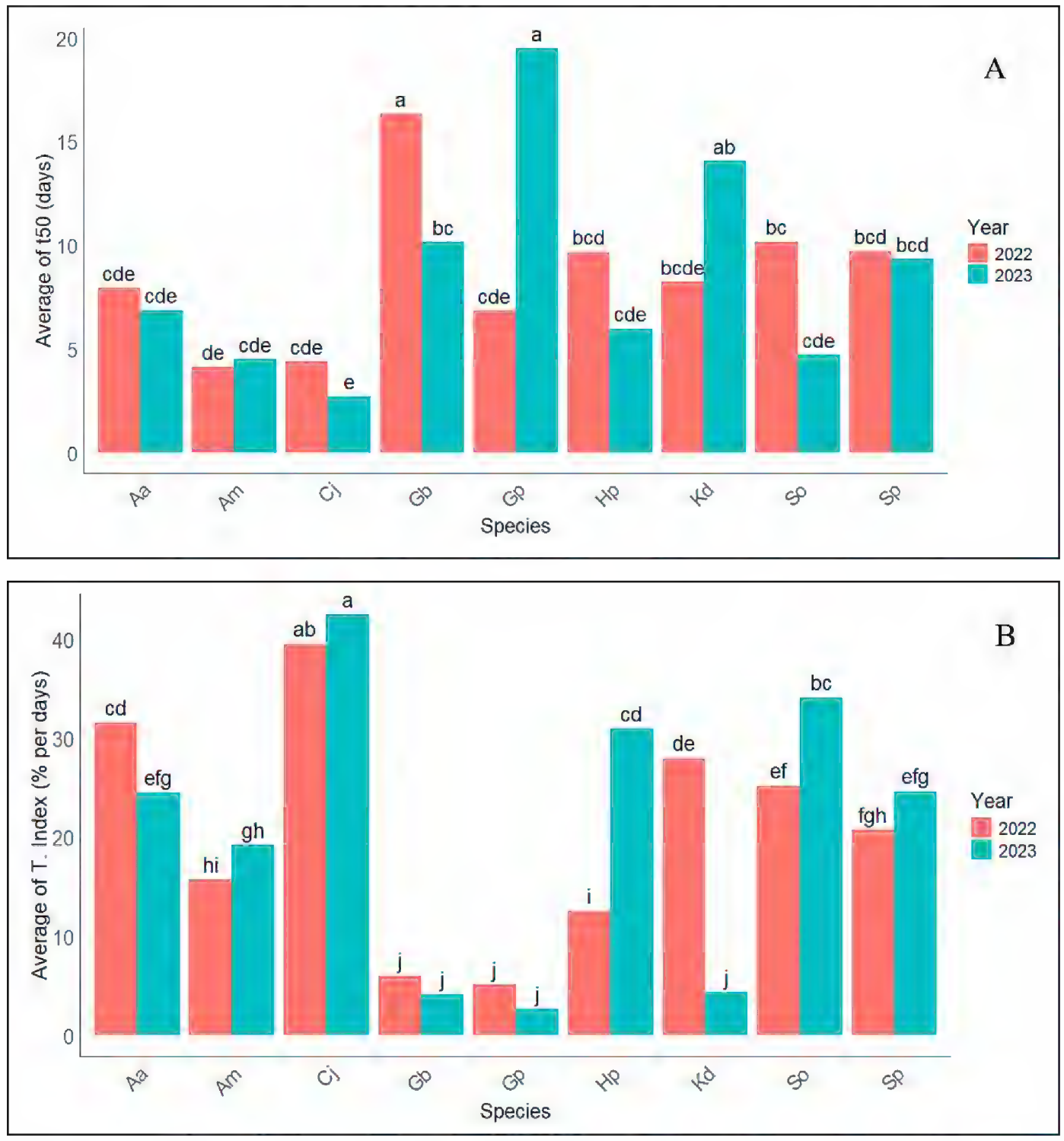
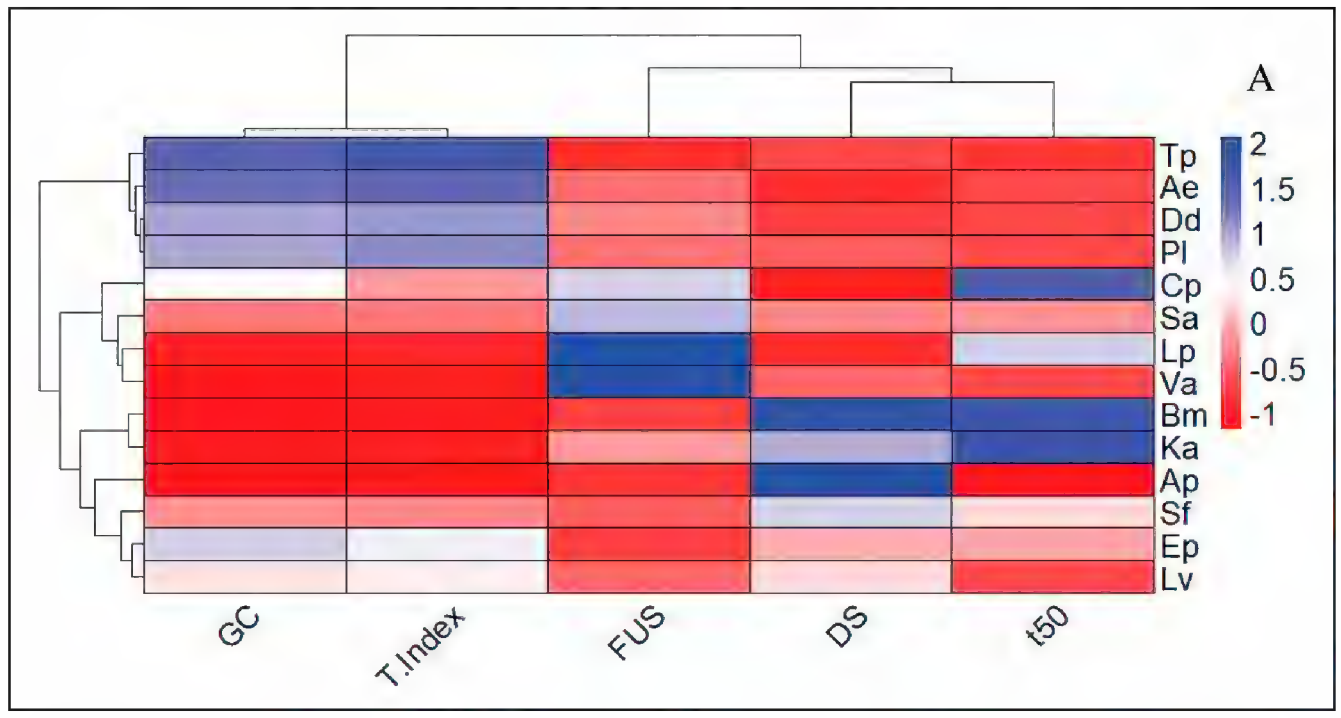


Figure 5. LSD bar plots of seed germination quality aspects of species collected in early October 2022 and late September 2023. **A.** t_{50} or the median germination time (days), and **B.** Timson Index (% per day). The same letter indicates non-significant differences according to LSD post hoc at $p<0.05$. The full names of the species are given in Table 1.

temperature in September 2022 (compared to 2023) resulted in faster germination rates for *K. dubia* seeds (T. Index 27.9% per day) and *A. angulosum* (31.6% per day), but the following year (2023) seeds of both species collected under drier and warmer conditions responded with significantly slower germination (4.3% per day and 24.5% per day, respectively). Additionally, the Timson Index of *H. perforatum* seeds in 2022 (12.5% per day) was more than twice as low as that of 2023 seeds (30.9% per day), indicating only small variations formed between the years studied.

b. Heatmap clustering seed germination parameters

Based on the z-score values in the heatmap, the germination performance in July 2022 (Fig. 6A) shows higher variability, highlighted by four species (*T. pratensis*, *A. elatius*, *D. deltoides*, and *P. lanceolata*) that have similarities of higher GC, faster T. Index, lower proportion of FUS and DS, and shorter t_{50} than others. In turn, species such as *L. pratensis* and *V. angustifolia* are grouped according to the highest content of FUS. Nevertheless, a longer t_{50} period, accompanied by a slower T. Index, was observed in *B. media* and *K. arvensis*. Compared to July 2023, this variability resulted in more uniform heatmap clustering, as some species showed changes in



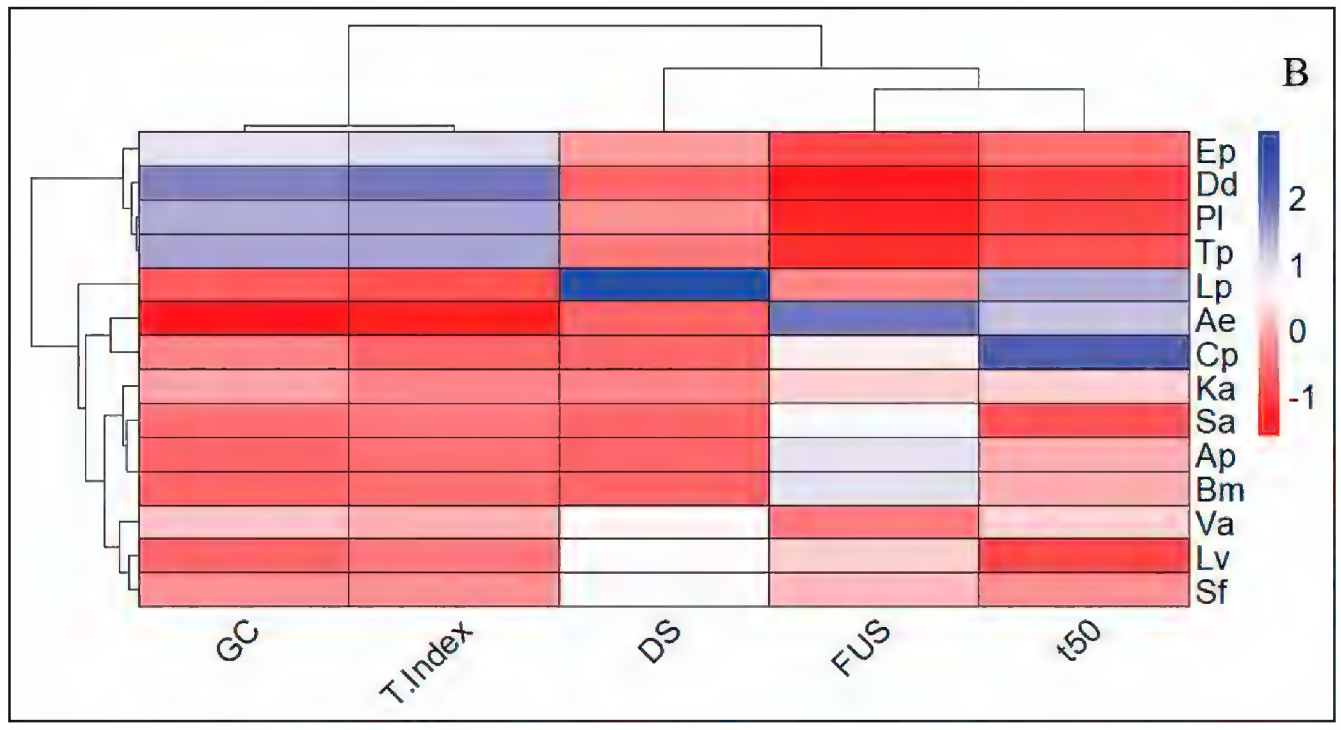


Figure 6. Heatmaps of the analysed germination parameters of seeds collected in July in two different harvest years. **A.** July 2022, and **B.** July 2023. The colour gradient represents values of z-scores from negative (red) to positive (blue), with lower values represented by darker red and higher values by darker blue. The full names of the species are given in Table 1.

their germination performance (Fig. 6B). *E. planum* changed the position of *A. elatius* in the group of species with the highest GC and the fastest T. Index.

Species collected in early October 2022 and late September 2023, such as *C. jacea* (highest GC and fastest T. Index) and *A. millefolium* (highest DS proportion), showed consistent germination performance in both years. However, changes in environmental conditions resulted in a shift of the two species with the highest germination efficiency in 2022 (*A. angulosum* and *K. dubia*) and 2023 (*H. perforatum* and *S. officinalis*) (Fig. 7A). Higher temperatures, along with lower rainfall in September 2023, led to a decrease in seed germination capacity (GC) and a decrease in germination velocity in *K. dubia* resulting in this species being grouped with *G. boreale* and *G. pratense*, and being among the species with the higher share of FUS and longer t_{50} in both clustering years (Fig. 7B).

c. Decision trees based on seed maturation periods

Decision tree analysis revealed that the Timson Index was the most important factor explaining GC. For seeds ripening in June and collected in July 2023, the resulting tree consisted of 2 terminal nodes and 1 secondary sub-branch (Fig. 8A). Firstly, the division was made according to the T. index (< 25% per

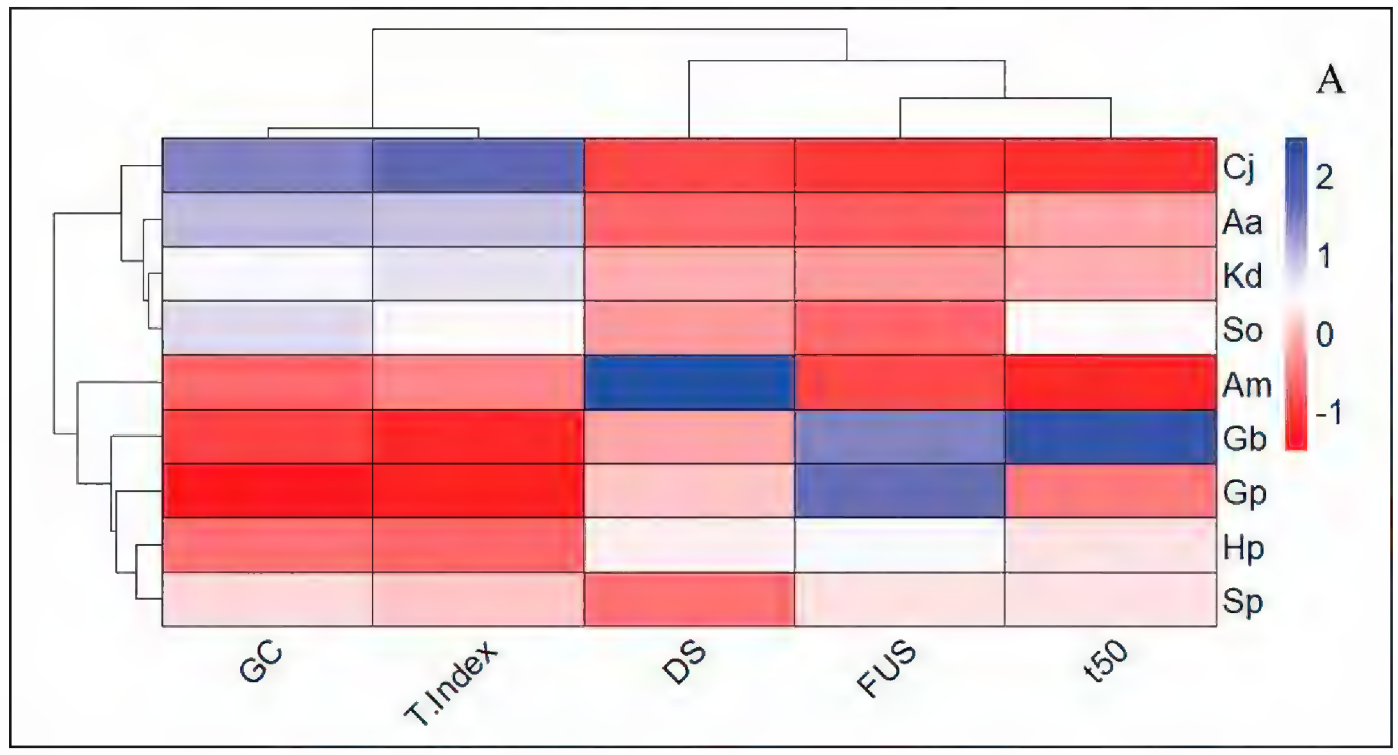


Figure 7. Heatmaps of the analysed germination parameters of seeds collected in September/October in two different harvest years. **A.** October 2022, and **B.** September 2023. The colour gradient represents values of z-scores from negative (red) to positive (blue), with lower values represented by darker red and higher values by darker blue. The full names of the species are given in Table 1.

day). The right branch consists of 13 experimental units with an average T. index of 25% per day or more, which is associated with the highest GC (from 46% to 89%). This number of experimental units is represented by five species, such as *V. angustifolia*, *T. pratensis*, *P. lanceolata*, *E. planum*, and *D. deltoides* (Fig. 8B). Then, the left branch divided into sub-branches with a T. index < 15% per day (right) resulted in the lowest proportion of GC (on average below 23%) represented in leaf 3 for eight species (*S. flos-cuculi*, *S. autumnalis*, *L. vulgare*, *L. pratensis*, *C. patula*, *B. media*, *A. pratensis*, and *A. elatius*) (Fig. 7B). Next, leaf 4 with moderate germination velocity (15%≤ T. Index < 25%) also has eight species.

The decision tree of species ripening in September and collected in late September 2023 branches only at two leaf nodes, except for *A. angulosum* at both nodes (Fig. 9). The first node is in leaf 2 and includes five species (*K. dubia*, *G. pratense*, *G. boreale*, *A. millefolium*, and *A. angulosum*) with a T. Index < 21% per day, indicating low average GC (Fig. 9A). The second node is also represented by five species (*S. pratensis*, *S. officinalis*, *H. perforatum*, *C. jacea* and *A. angulosum*) with a T. Index ≥ 21% per day, reflecting high mean GC (between 27 and 75% and above 75%) (Fig. 9B).

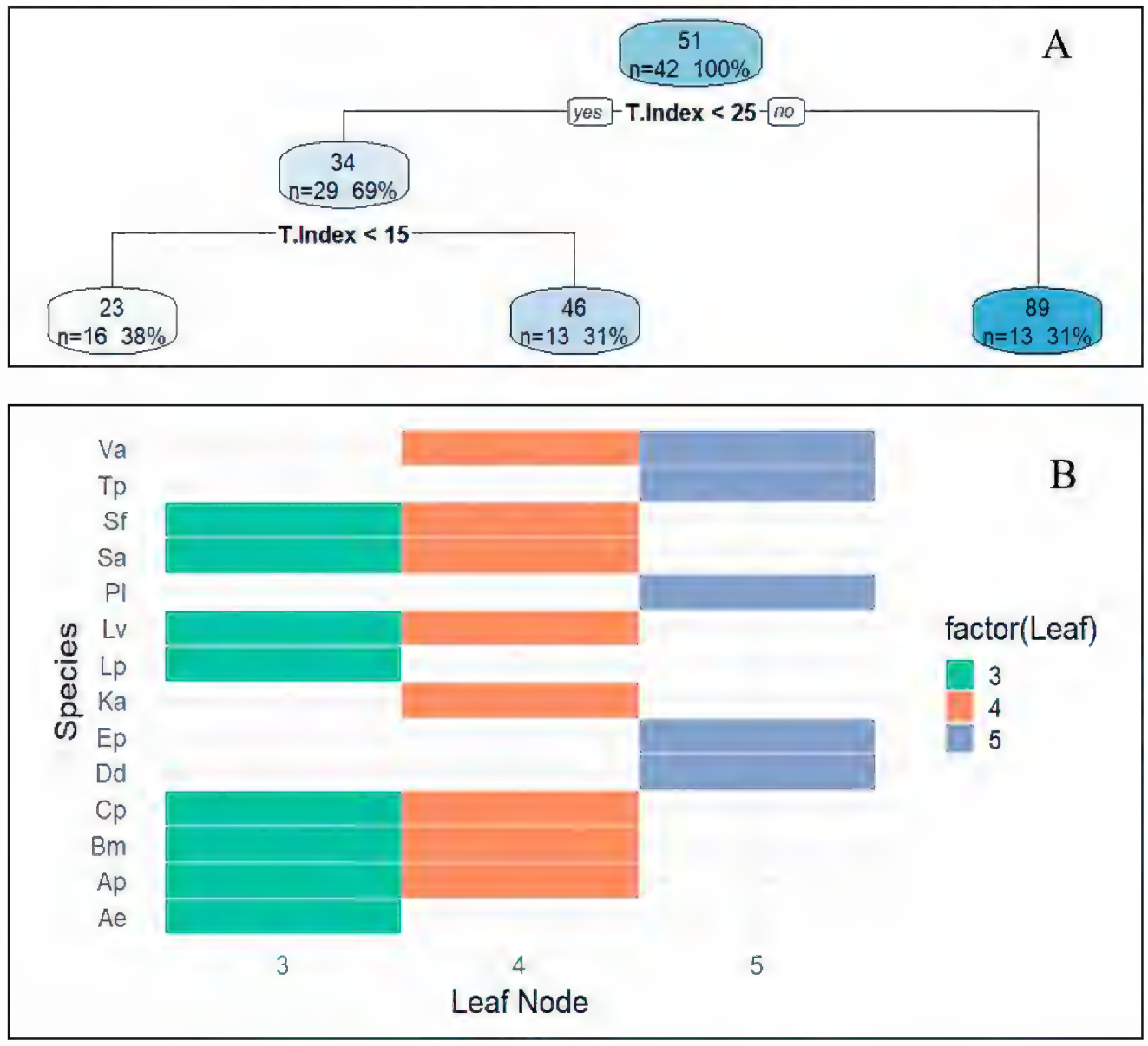


Figure 8. Decision tree for species collected in July 2023. **A.** Decision tree split, and **B.** Species covering every leaf node. The full names of the species are given in Table 1.

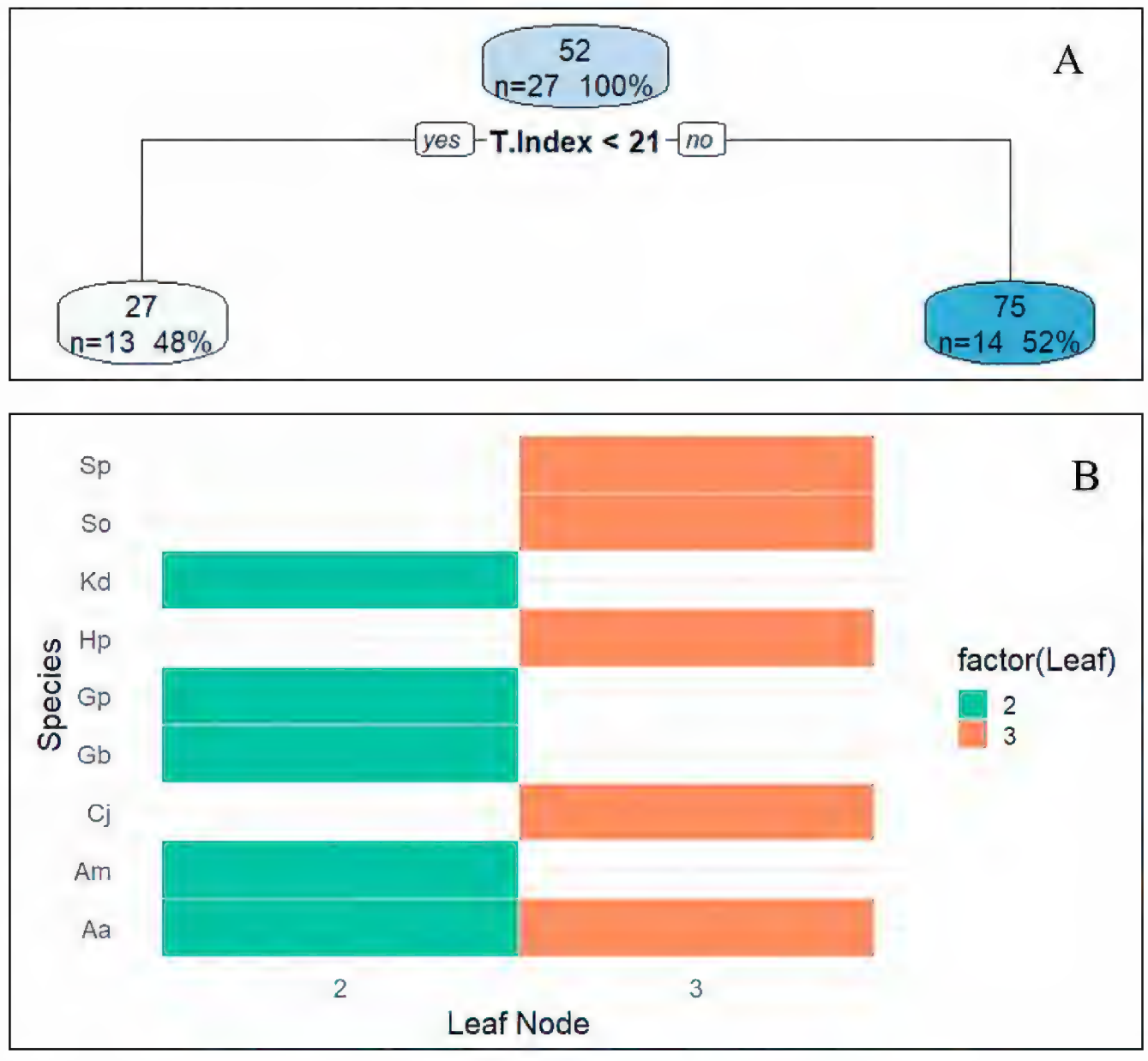


Figure 9. Decision tree for species collected in late September 2023. **A.** Decision tree split, and **B.** Species covering every leaf node. The full names of the species are given in Table 1.

Discussion

In the present study, we demonstrated intra- and interspecific variability in germinabilities over the years, both within and between species, from the same or different botanical families. These results strengthened the previous findings of Bhatt et al. (2018), Veselá et al. (2021), Zettlemoyer and Lau (2021), and Vázquez-Ramírez et al. (2025), who concluded that these germination variations can be expressed as a maternal effect on progenies since discrepancies of temperature, rainfall, and nutrient supply experienced by mother plants acted as phenotypic plasticity. Other studies by Janicka et al. (2021) on 28 species collected from different plant communities in lowland hay meadows and by Vázquez-Ramírez et al. (2025) on 3 native Alpine species also revealed a relationship whereby the progeny from the warming period showed slow germination and poor or even lack of seedling performance due to insufficient nutrient supply, resulting in a shortened generative stage and the production of unviable seeds.

Veselá et al. (2020) found that the maternal effect on germination control can be altered by photoperiod strategy in the laboratory. This was shown by Nguyen et al. (2021) that maternal effect could be changed by altering the photoperiod regime in *Petunia* x *hybrida* tested with a photoperiod of 16 h (light)/8 h (dark) under a fluorescent white lamp at 25 °C in a germination test, and then changing the photoperiod to 14 h (light), and temperature in the range from 22 to 31 °C, which resulted in a decrease in the germination percentage and an increase in the ABA synthesis by a de novo physiological mechanism. Another germination study on salinized grassland species in Northeastern China by Zhao et al. (2021) proved that the temperature range of 18 to 25 °C under a 12 h (light)/12 h (dark) photoperiod was more important for achieving significant germination percentage and time, regardless of the seed maturation time of the species. The high maximum temperature limit used in our study (30 °C) may have led to rapid ABA synthesis, resulting in a high proportion of FUS and DS in several species. Further research may indicate the optimal temperature range for germination testing, particularly for species found in lowland hay meadows.

The greater variability in seed germination of forbs over the years may be attributed to the life cycle and species characteristics (Dalgleish et al. 2010). Thus, some plants with a short-flowering period were more sensitive to variable weather conditions during recruitment than plants with a long-flowering period, such as *T. pratensis*, *C. jacea*, *S. officinalis*, and *S. pratensis*. Price et al. (2023) explained that intra-specific variability can be formed by environmental gradients for forbs seed germination, even with similar temperature requirements, and this variability in response to specific temperatures should be considered when determining the sowing date. Thus, shifts in the temperature ranges necessary for germination also affect the level of dormancy, which some plants can expand or narrow within their favourable environmental range depending on the weather in the following year (Kildisheva et al. 2019).

The pattern of germination dynamics can be complemented by considering germination time as a cumulative response to temperature changes (Ghaleb et al. 2022). Our study included an assessment of germination time and velocity, because any change in germination time (t_{50}) directly affected the velocity discrepancies (Caser et al. 2022). Some native species of lowland hay

meadows, such as *K. arvensis*, *L. pratensis*, and *G. pratense*, showed shortened t_{50} for seeds collected in 2023. The seed filling and ripening processes of the two above-mentioned species, collected in July (*K. arvensis* and *L. pratensis*), seem to reach optimal ripening with only a slight increase in temperature and rainfall. In turn, a decrease in total rainfall, followed by the highest temperature increase in 2023, from August to September, may stimulate the maturation of *G. pratense* seeds. This phenomenon revealed a mechanism of plasticity related to the germination niche that can be used to guide the restoration and conservation of local species (Price et al. 2023).

For conservation purposes, germination potential and germination probability are utilised as tools to support guidance on sowing dates, including both sowing time and species selection (Price et al. 2023). This approach has also been implemented in Slovenian dry meadows (dry to semi-dry calcareous grasslands of the *Festuco-Brometea* class, habitat code 6210 in Annex I), where *in-situ* conservation is carried out by maintaining native species communities by composing a variety of threatened and native, climate-resilient species for sowing, rather than single species (Bavcon et al. 2024). Especially in the face of climatic problems affecting seed progeny, species with the highest germinability and the shortest germination time, such as *T. pratensis* and *C. jacea*, may be prioritized in the establishment of plant structures enriched with local grasses (*A. elatius*, *A. pratensis*, and *B. media*) to a greater extent to cover the empty spaces (voids) in the soil, thus providing an ecological niche (Carta et al. 2022). For native taxa of legume, the use of perennial (*L. pratensis*) may benefit for providing ecosystem services compared to annual ones (*V. angustifolia*) considering their longevity in sward (Rantala-Sykes and Campbell 2019). Scotton (2016) assessed the species ratio pattern among dominant grass species, followed by legumes and forbs, as a key factor in maintaining the sustainability of protected Italian *Arrhenatherion* meadows after 5 years of restoration.

Toma et al. (2023) explained that conservation can guide restoration goals in defining desirable reference habitats. In European semi-natural grasslands, high rates of biodiversity loss due to land-use change and climate change have resulted in the aggregation of existing species into fragmented and isolated patches, which has reduced the population of reference habitats (Picó and van Groenendael 2007). One possible way to enable local species to revegetate is to reduce pathways between fragmented populations by sowing seeds or introducing new seedlings. Therefore, the focus should be on local species that can germinate at a high percentage and in a short time, as shown in the decision tree analysis. Both the GC and the Timson Index can be used as basic criteria for selecting the species studied. Species with such abilities can occupy open spaces and avoid undesirable plants (Barr et al. 2017).

Several issues related to the introduction of selected species with respect to seed quality should be considered (Ontivero et al. 2024), so that our decision trees position some species on two branches (low to medium GC and T. Index or medium to high GC and T. Index) to clearly express the germinabilities of the species. Unfortunately, this pattern (low to medium GC and T. Index) was observed in several species characteristic of lowland hay meadows (*L. vulgare*, *C. patula*, *B. media*, *A. pratensis*, and *A. angulosum*), also a native legume such as *L. pratensis* (low GC and T. Index), listed in Council Directive 92/43/EEC, and on the official website of the EEA (European Environment Agency) (EEA 2019).

These species are characteristic of Natural Habitats of Community Importance (NHAs) that require restoration, such as *Arrhenatherion elatioris* (6510), *Molinion* (code: 6410), and *Cnidion dubii* (6440). Therefore, this information can be helpful in guiding conservation and restoration efforts by ecological practitioners, such as determining the optimal time to collect seeds of native species, increasing germinability, and selecting species for seed mixtures (Delicour et al. 2023). These conservation-oriented restoration approaches are expected to optimize the use of native and/or threatened plant species for restoration, while ensuring that their ecosystem value in the targeted habitat is prioritised (Volis 2019). This mechanism offers an alternative contribution to achieving the 10% increase in the EU biodiversity target by 2030.

Overall, the species migration from the heatmap plots, characterised by unstable germination efficiency during the two years studied, can provide us with information about the adaptive mechanisms of *Arrhenatherion* meadow species in response to climate fluctuations (Veselá et al. 2021). Thus, the low availability of native seeds of adequate quality, caused by climatic factors and maternal effects, can be overcome by ex-situ conservation, which maintains their stable germinability and establishment capacity, and provides a larger number of progenies for large-scale restoration (Shen et al. 2016). Additionally, future studies on germination dynamics should consider other factors, such as seed storage, seed viability, and variation in photoperiod regimes, to gain a better understanding of the germination processes of local native species (Kolb et al. 2016). In this way, such future research can ensure the availability of high-quality seed sources in sufficient quantities for long-term conservation and restoration.

Conclusions

Weather shifts during the seed ripening affect the seed germination efficiency. Seeds of *A. elatius*, *C. patula*, and *L. vulgare* (collected in July) and *A. angulosum*, *G. boreale*, and *K. dubia* (collected in late September/early October) responded most strongly to these changes. Wetter weather conditions during seed ripening contribute to an increase in the FUS and a decrease in the DS, as well as to an extension of the t_{50} period and a decrease in the Timson Index for most species. Meanwhile, warmer and drier weather causes a decrease in the FUS index, an increase in DS, and an extension of the t_{50} period, but has a smaller effect on the Timson Index (only 4 of 23 species: *A. angulosum*, *G. boreale*, *G. pratense*, and *K. dubia* had a decrease in this index). Species with stable quantity seed germination (GC, FUS, and DS) and quality traits (t_{50} and Timson Index) in both study years were *T. pratensis*, *D. deltoides*, and *P. lanceolata* (collected in July) and *C. jacea* (collected in September/October). These species can be recommended for rapid revegetation and conservation of local, native *Arrhenatherion* meadow species. Furthermore, it was indicated that the Timson Index can serve as a basic parameter for assessing the germination process, explaining seed germination efficiency, and facilitating the selection of introduced species. For conservation-oriented restoration, species with stable values of both parameters (GC and Timson Index) can be prioritised for inclusion in seed mixtures, which are then supplemented with local native species that provide specific ecosystem services.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: MJ, FAP. Data curation: FAP. Formal analysis: FAP. Funding acquisition: FAP. Investigation: FAP. Methodology: FAP, MJ. Project administration: FAP. Resources: MJ. Software: FAP. Supervision: MJ. Validation: MJ. Visualization: FAP. Writing - original draft: FAP. Writing - review and editing: MJ.

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Data availability

All of the data that support the findings of this study are available in the main text.

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